

ON THE DISTRIBUTION OF A MARINE CLADOCERAN, *PENILIA*  
*AVIROSTRIS* DANA (CRUSTACEA, BRANCHIOPODA), WITH  
A NOTE ON ITS REPORTED BIOLUMINESCENCE

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The marine cladoceran, *Penilia avirostris* Dana, is a member of the surface plankton found in warm and temperate coastal waters at widely scattered points throughout the world. Its recent regular appearance in the waters around Woods Hole, Massachusetts, far to the north of its previously supposed temperature limits, has prompted the writing of the present paper. From a survey of the literature it was found that the reported distribution of *Penilia* poses a number of problems of exceptional interest. These problems are here discussed, and the results are reported of certain observations made on living specimens of *Penilia* at Woods Hole. No very definite conclusions have been reached, but it is hoped that other investigators will continue the study, since *Penilia* would appear to be an organism offering certain special advantages to the student of plankton distribution.

COLONIZATION OF THE SEA FROM FRESH WATER

Of all planktonic marine organisms *Penilia* is perhaps the easiest to identify, for it is the sole marine representative of the cladoceran tribe Ctenopoda, characterized by six similar pairs of filter-feeding trunk appendages enclosed by a bivalve carapace. Indeed even in the related tribe Anomopoda (in which the trunk appendages are not all alike) there are no marine representatives, other than *Bosmina maritima*, found only in the Baltic. Two other cladoceran genera, *Podon* and *Evadne*, are marine, but are members of the aberrant family Polyphemidae, in which the much reduced carapace does not cover the somewhat leg-like trunk appendages. At the present time only a single species of *Penilia* is recognized (see Steuer, 1933a), so that the task of picking *Penilia* out from a plankton sample can be assigned to anyone capable of using a microscope.

Among the many hundred species of filter-feeding Branchiopoda, *Penilia* alone is truly marine. Yet in the other classes of free-swimming Entomostraca, namely the Branchiura, Ostracoda, and Copepoda, we find a much more even distribution of species between marine and fresh water habitats. One might infer that perhaps it is the possession of leaf-like trunk limbs, or "phyllopodia," which has tended to exclude Branchiopoda from marine environments. Storch (1925) and others have pointed out that the effective shape of phyllopodia, and indeed of other parts of the body in these animals, is dependent on the pressure of the blood in the hemocoel. In a fresh water environment this pressure, or state of turgor, can be maintained by a simple osmotic inflow of water. In salt water, maintenance of the turgor would

be more difficult. Despite this fact, however, there are a few species, in each of the four orders of Branchiopoda (Anostraca, Notostraca, Conchostraca, and Cladocera), which have colonized saline pools (see, for example: Mathias, 1937; Packard, 1883, p. 369; Parenzan, 1932). In the case of the anostracan, *Artemia*, Kuenen (1939) has shown that the blood is always hypotonic to the surrounding saline medium; the turgor of the blood in this animal has to be maintained by an active transfer of water against the osmotic gradient; if the animal becomes unhealthy it soon loses its plump appearance and shrinks in volume. In the case of the cladoceran, *Daphnia magna*, which can be acclimatized to quite high salinities, the blood is kept hypertonic to the surrounding medium, thus favoring an osmotic inflow of water (Krogh, 1939).

Although thus able to withstand high salinities, these Branchiopoda which can live in saline pools have never been successful in colonizing the sea. They are adapted to life in shallow, often temporary waters, and seem unable to survive in the very different conditions met with in the ocean.

The ancestor of *Penilia* must have migrated from fresh water to the sea through some favorable river estuary. Its closest relatives, including especially the genus *Sida* (see Lochhead, 1936-7), live chiefly in lakes rather than in small pools. As in other filter-feeding Branchiopoda, the shape of the phyllopodia and other parts of the body in *Penilia* doubtless depends on the maintenance of internal turgor. Specimens of *Penilia* which have sunk to the bottom of a container have a bedraggled appearance, in contrast to the plump specimens still swimming actively in the water above. It is not known whether the internal turgor is achieved by an active transport of water, as in *Artemia*, or by keeping the blood hypertonic, as in *Daphnia*. Fox (1952) reports that *Penilia*, in common with other small Crustacea, constantly ingests water, through both the mouth and the anus. Much of the ingested water seems to be absorbed, but Fox doubts that this is the primary mechanism for maintenance of internal turgor.

*Podon* and *Evadne* do not have phyllopodia, their limbs being more like those of ostracods. It may be that the shape of these animals is not so dependent on internal turgor as in other Branchiopoda. In this connection it is perhaps significant that in the family Polyphemidae, to which *Podon* and *Evadne* belong, there are more species in salt than in fresh water.

*Penilia*, *Podon* and *Evadne* share in common two features of the reproductive system that are not found in a majority of other Cladocera. Perhaps, therefore, these are features that in some way have proved helpful in the colonization of the sea, though in just what way is not very evident. The fertilized, resting eggs have thick shells, and are not enclosed in a protective "ephippium." The eggs which develop parthenogenetically are small, almost devoid of yolk, and during embryonic development increase greatly in size by absorption of a nutritive fluid secreted by the mother into the brood sac. This last feature is characteristic of both fresh water and marine Polyphemidae, but it is not known for any Ctenopoda other than *Penilia* (Storch, 1925; Sudler, 1899). Perhaps it is no more than a coincidence that the same feature is found also in the anomopod genus *Moina*, species of which are among the Cladocera most frequently encountered in saline pools.

## SPORADIC AND DISCONTINUOUS DISTRIBUTION

Information available to date indicates that *Penilia* has an extremely sporadic and discontinuous distribution. It has been recorded from the shores of every continent, frequently in tremendous numbers, but from widely separated points and often only during a single season. At Beaufort, North Carolina, Sudler found *Penilia* in June, 1896, in such numbers as to clog a net towed for only a few meters through the water. Not until 1931 was *Penilia* again recorded from our Atlantic coast, when it was taken off New Jersey (Bigelow and Sears, 1939). Dr. R. E. Coker very kindly informs me that he later found a single specimen in plankton taken outside Beaufort Inlet, in January, 1949, and that a number of specimens were taken there towards the end of 1953. At Naples, Italy, *Penilia* was unknown until 1922, when Caroli found it throughout the summer, the population becoming so large in late August as to form practically the entire surface plankton. In this case the population became established, and *Penilia* has since reappeared at Naples in large numbers each summer (Cattley and Harding, 1949). In the waters off Sydney, Australia, *Penilia* has been recorded on various occasions since 1894, and recently its volume there was so great (0.85 ml./m.<sup>3</sup>) as to constitute the richest haul of non-salp plankton taken in Australian waters (Sheard, 1949). This compares with the best hauls of non-salp zooplankton commonly taken in temperate northern waters, although volumes of over 5 ml./m.<sup>3</sup> have been recorded (Clarke and Bishop, 1948).

Further examples could be cited, but enough has been said to show how suddenly *Penilia* may appear, and the abundance it may attain. The periods of abundance are always associated with a high rate of ovoviviparous parthenogenesis, as in other Cladocera, but the fluctuations must be correlated with as yet unknown environmental factors. Since *Penilia* can be so easily identified, has a direct development uncomplicated by larval stages, and has feeding habits that are reasonably well known (Lochhead, 1936-7), it should be a favorable species for a study of factors underlying such seasonal fluctuations in abundance as are discussed by Sears and Clarke (1940).

An incomplete summary of the discontinuous world distribution of *Penilia* has been given by di Caporiacco (1938). Additional records will be found in some of the references listed at the end of the present paper. No simple explanation is evident for this discontinuous distribution, nor for the sporadic appearances of *Penilia*. In the case of fresh water Cladocera, examples of the same kind can be explained by assuming a chance distribution of resting eggs, especially on the feet of birds, to isolated bodies of water. Coastal waters of the oceans are, however, continuous, and opportunity for the resting eggs of *Penilia* to become attached to the feet of birds would not appear to be great. The resting eggs of Ctenopoda and Polyphemidae are generally said to be cast loose into the water. Weismann (1877) found those of fresh water species lying at the bottom of aquaria. It also has been supposed that the resting eggs of *Penilia*, *Podon*, and *Evadne* sink in sea water (Bigelow and Sears, 1939; Friedrich, 1952). However, Jorgensen (1933-4) found the resting eggs of *Evadne nordmanni* in surface plankton, enclosed in the parental exuviae. She suggests that they may not sink as rapidly as had been supposed.

They might then be dispersed widely by currents, in spray by the wind, and to beaches where they could be picked up on the feet of birds. It seems unlikely, however, that such a condition holds true for *Penilia*. Caroli (1924), who followed throughout a summer a population of *Penilia* with a relatively high output of resting eggs, never saw these eggs enclosed within exuviae. He concluded that the eggs probably sink to the bottom. Possibly the sudden appearance of *Penilia* in new localities occurs only when a few recently released resting eggs, that have not yet had time to sink, chance to have been caught up in wind-driven spray.

More difficult to explain is the apparent absence of *Penilia* from many intermediate locations. This might seem to indicate that *Penilia* has only recently invaded the sea. If that were true, however, one would expect to find *Penilia* especially abundant in river estuaries, whereas it more usually is found in open coastal waters. Perhaps unsuspected environmental factors have excluded *Penilia* from certain areas. Or it may be that populations in some areas have died out during parthenogenetic reproduction through the action of dominant or semi-dominant lethal genes. Instances of this kind have been recorded by Banta and Wood (1939) for some fresh water Cladocera. Banta (1939) notes that there are wild populations of certain fresh water Cladocera which are never known to reproduce other than by ovoviviparous parthenogenesis. In one case he found a mutant stock in which both resting and "summer" eggs were produced by parthenogenesis. It may well be that in some areas *Penilia* reproduces only by parthenogenesis, probably then without the production of resting eggs. Information on this question is very scanty, since most of the reports dealing with *Penilia* fail to mention the sexes taken or the type of reproduction observed. Steuer (1933a, 1933b) stated that males were at that time known only from Hong Kong, Naples, the Adriatic, and the Black Sea. In the literature I have found only one additional record that seems to refer to the occurrence of males. Dakin and Colefax (1940) state that off Sydney, Australia, *Penilia* was "found breeding in April and May." Since this was at the end of the season, and maximum numbers of *Penilia* were noted in January and February, it seems probable that the statement was meant to refer to bisexual reproduction. One more locality for the occurrence of males and resting eggs can now be added, namely, Woods Hole, Massachusetts, where in August, 1953, I found about one or two per cent of the population of *Penilia* to be males, and a lower percentage to be females bearing resting eggs.

Obviously, further records are needed before any conclusions can be drawn as to the prevalence of males and resting eggs in different localities. It would be helpful if those who record the presence of *Penilia* would always take care to state what types of individual were found. Steuer (1933b) figures juvenile instars and the three types of adult, namely, males, females with one or two resting eggs, and parthenogenetic females with "summer" eggs or embryos. "Summer" eggs which have not yet developed into embryos are much smaller than resting eggs, and in most cases are more numerous. Persons not having access to Steuer's paper should be able to identify the different types of adult by reference to Figure 1, which shows a female bearing a single resting egg, and a male one instar prior to maturity. Mature males have penes over twice the length of those shown, and antennules reaching to the posterior border of the carapace. Males two instars prior to maturity can be recognized



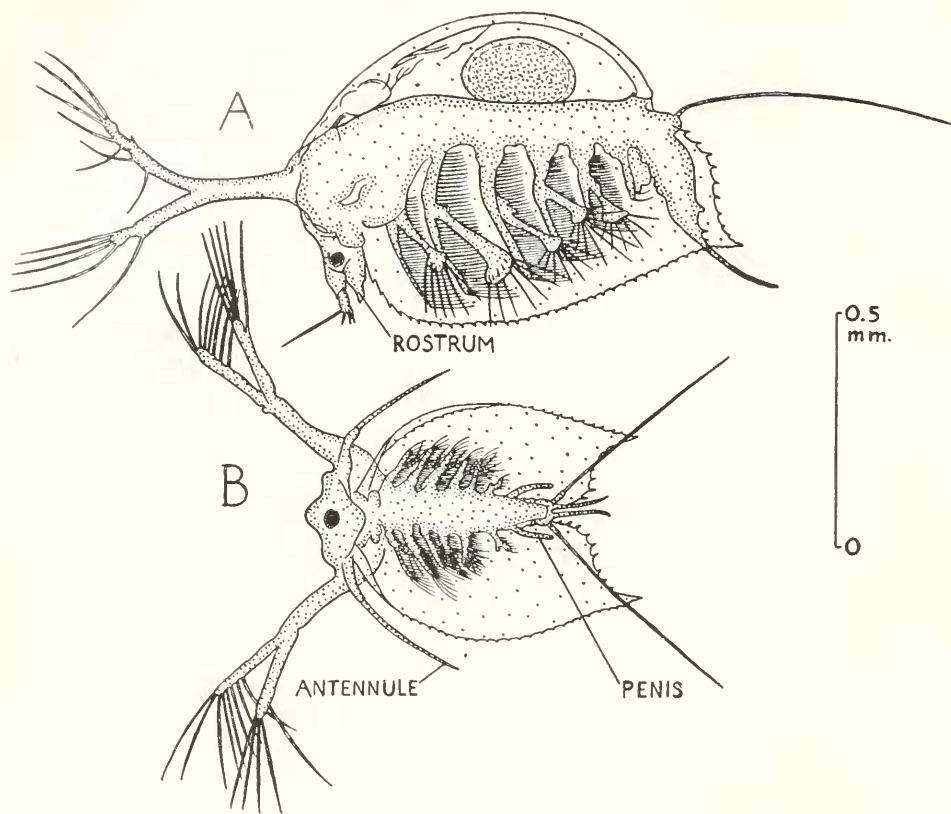


FIGURE 1. *Penilia avirostris* Dana, from Woods Hole, Massachusetts, August, 1953. Sketched from preserved specimens, a camera lucida being used for the main outlines. A, mature female, with a single resting egg in the brood sac; B, male one instar prior to maturity; the shell valves are here much wider apart than they would be in a living specimen.

by small rudiments of the penes, antennules already twice the length of those in a female, and, as in all males, by the absence of a pointed rostrum.

#### RESTRICTION TO COASTAL WATERS

The restriction of *Penilia* to coastal waters is another feature for which no definite explanation can be offered at present. The greatest distances from shore at which *Penilia* has been taken seem to be those reported by Bigelow and Sears (1939) (about 60 km. off the coast of New Jersey) and by Marukawa (1921) (either about 230 km. or about 310 km. east of Japan). Neither temperature nor salinity would appear to be a factor excluding *Penilia* from the open sea. Some authors have spoken of *Penilia* as a predominantly brackish water form (e.g., Gibitz, 1922). There has even been a single isolated record of *Penilia* from fresh water (Krämer, 1895). However, most of the records of *Penilia* have been from localities with salinities above 32‰. Leder (1915) found *Penilia* in salinities from 10‰

to 37‰. Della Croce (1952) found maximum numbers of *Penilia* in the Gulf of Genoa when the salinity was above 38.3‰. Gurney (1927-9) found *Penilia* abundant in the Gulf of Suez where the salinity was 43.8‰, and even recorded it from a station in the Suez Canal where the salinity was 49‰ (salinities taken from Fox, 1926-9). It is evident that the salinity of the open ocean lies well within the range normally tolerated by *Penilia*. At low temperatures, however, the resistance to high salinities may be reduced, in accordance with Moore and Kitching's (1939) "idea of modified tolerance." Thus Dakin and Colefax (1940) found *Penilia* four miles out to sea off Sydney, Australia, reaching maximum abundance in summer, yet also found it to be sometimes exceedingly abundant in winter in the more estuarine catches. This is despite the fact that minimum surface water temperatures were lower in the estuary (12.3° C.) than at the offshore station (15-16° C.) (Dakin and Colefax, 1935). Salinity at the offshore station was 35.4-35.8‰; that within the estuary was unfortunately not given.

Perhaps the restriction of *Penilia* to coastal waters is a result of a shortage in the open sea of fine detritus and minute organisms, under 5  $\mu$  in diameter, on which *Penilia* feeds (Lochhead, 1936-7). However, other animals requiring equally fine food do live successfully in the open ocean.

If it should be found that populations of *Penilia* must everywhere be renewed each year from resting eggs, and if these eggs sink to the bottom, as seems probable, then the restriction of *Penilia* to waters of moderate depth would be understandable. However, in tropical regions one would expect at least some populations to be successful in reproducing throughout the year exclusively by ovoviviparous parthenogenesis.

#### RESTRICTION TO SURFACE WATERS

Apparently *Penilia* always occurs relatively close to the surface. Gamulin (1948-9) records it from depths of 20-70 meters in the Adriatic; Motoda and Anraku (1952) found it only at depths of 10-20 meters in "Funka Bay," Hokkaido, Japan (apparently a synonym for Volcano Bay, judging from a map (Fig. 4) in Kawasaki *et al.*, 1952-3). Nearly all other records seem to have been from surface plankton tows.

I have tested the reactions to light of specimens of *Penilia* taken at Woods Hole, with purely negative results. When illuminated only from one side by a bright, horizontal beam of light from a spot lamp, *Penilia* continued to swim in various directions in all parts of a jar, whereas copepods in the same jar quickly aggregated towards the light. Specimens of *Penilia* also swam at random, both upwards and downwards, when illuminated only from above; the spot lamp was placed 23 cm. above a small tube, holding a column of water 60 mm. high and 18 mm. in diameter, standing on a dull black surface. Copepods tested under these same conditions aggregated immediately towards either the top or the bottom of the tube, depending on the species, in contrast to *Penilia* which showed no such tendency even over periods of up to fifteen minutes. In both the horizontal and the vertical beams of light results were the same with light-adapted *Penilia* and with *Penilia* which had been kept in total darkness for periods of from one to twelve hours. In all cases the specimens spent much time floating suspended in the water, swimming in sudden spurts at irregular intervals, as is characteristic for

the species. Neither when floating nor when actively swimming could the specimens be seen to show any type of dorsal light response to the direction of illumination. It may be concluded that the restriction of *Penilia* to surface waters would appear not to be in response to light.

Nor does it seem that this restriction depends on a response to pressure, of the type discovered in crab larvae by Hardy and Bainbridge (1951). To test for such a response, specimens of *Penilia* which had been kept in the dark for twelve hours were transferred to a 10-ml. syringe, over the lower opening of which a piece of wax paper had been tightly tied. The level of sea water was adjusted up to the mark and the plunger then very slowly pushed down until all air had been expelled. With the lower end of the syringe resting on a table, pressure on the plunger was now increased steadily by hand up to a maximum later found equal to about 10.5 kilograms. Since the internal diameter of the syringe was 14 mm., it can be computed that the maximum water pressure attained, additional to atmospheric pressure, was approximately 6.8 kg./cm.<sup>2</sup>, corresponding to a depth in the sea of about 67 meters. The specimens of *Penilia* in the syringe were observed against a brightly lighted dark background. At all pressures they continued to swim normally, showing no tendency to aggregate at any particular level in the column of water.

It must remain for the future to determine what factors may be responsible for the restriction of *Penilia* to surface waters. Perhaps a response to temperature is involved, or perhaps under some conditions the animals display negative geotaxis. However, no evident responses to gravity were seen in the specimens observed in vertical tubes.

#### DISTRIBUTION AS RELATED TO TEMPERATURE

The distribution of *Penilia* towards the poles is limited by temperature. Calman (1917-23) stated that the mean annual surface isotherms of 18° C. would include all localities where *Penilia* had been found, except for Trieste, the Black Sea, and possibly New Zealand. This statement remained unchallenged for many years, and it therefore was with considerable surprise that in 1944 I recognized what appeared to be a drawing of *Penilia* among some sketches of plankton organisms turned in by a student in the Invertebrate course of the Marine Biological Laboratory, Woods Hole, Massachusetts. The specimen was dead when found, and had been thrown away after being drawn. In 1946 a plankton sample collected for the Invertebrate course contained considerable numbers of *Penilia*, which I was able to examine alive. The same was true in 1948, 1949, 1951, 1952, and 1953. The samples each year were collected from the surface waters of Great Harbor, Woods Hole, between August 23rd and August 31st, with additional samples in 1953 from July 29th to September 1st. No especial search for *Penilia* was made in any year, so that it is quite likely that *Penilia* has been present in Woods Hole waters each year since 1944. Mr. A. Fleminger, a graduate student at Harvard University, has kindly turned over to me some specimens of *Penilia* taken in surface plankton from Menemsha Bight, Martha's Vineyard, about 20 km. S.S.W. of Woods Hole, July 25, 1951 (one specimen) and September 1, 1951 (25 specimens). Deevey (1952a, 1952b) has recorded the presence of *Penilia* in Block Island Sound, about 90 km. W.S.W. of Woods Hole, in 1943, 1944, 1945, and 1949.

One of her hauls in September, 1943, yielded about 2900 *Penilia* per fifteen-minute tow; another haul in October, 1949, yielded 900 *Penilia* per cubic meter.

Thus it is evident that at least since 1943 *Penilia* has occurred, often in large numbers, off the southern coast of New England. It must be a recent arrival, since it is not mentioned in any of the plankton surveys of the region made prior to 1943. As already noted, most of the specimens seen by me have been females, reproducing when adult by ovoviviparous parthenogenesis. One large specimen contained 13 embryos, a number which exceeds both the observed and the predicted maxima given by Steuer (1933b).

To gain more precise knowledge of the lower temperature limits controlling the distribution of *Penilia*, I have gathered together the information given in Table I. In my search of the literature I have not been able to find any records of *Penilia* from localities farther north or farther south than those shown in this table. It will be seen at once that the mean annual surface temperature at Woods Hole lies far below the limit of 18° proposed by Calman, or the limit of 17° more recently proposed by Fuller (1950). However, it will also be seen that *Penilia* has been taken from four other localities with mean annual surface temperatures well below these limits.

Actually, as pointed out by Hutchins (1947), the poleward distribution of marine organisms is controlled, not by the mean annual surface temperature, but by the lowest temperature tolerated in winter and by the minimum temperature necessary for reproduction in summer. Neither of these temperature limits is known for *Penilia*. Fuller (1950) thought that *Penilia* requires a temperature of at least 18–20° during a period long enough to permit reproduction. This suggestion agrees well with most of the records that we have for *Penilia*. However, Cattle and Harding (1949) found *Penilia* reproducing in October off the coast of Holland, in water of 16.68°. Possibly on occasion even lower temperatures would suffice, judging from the statement of Dakin and Colefax (1940) that in estuarine waters near Sydney, Australia, *Penilia* sometimes becomes exceedingly abundant in winter, when surface water temperatures of about 12–15° might be expected (Dakin and Colefax, 1935).

At Woods Hole the surface water temperatures in summer should more than suffice for the reproduction of *Penilia* (means for July, August, and September in the period 1945–1951: 21.3°, 21.8°, and 20.0°). The temperatures encountered in winter, however, are much lower at Woods Hole than in most of the other localities from which *Penilia* has been recorded. Reference to Table I will show that only in three of the other localities are the surface water temperatures in winter nearly as low as at Woods Hole.

In regions where the population of *Penilia* has been followed through a season, it is known that during the autumn the numbers gradually decrease to zero. The lowest temperature at which a surviving adult has been taken appears to be 8.7° (Steuer, 1933b). Usually all specimens are gone at temperatures well above that value. Survival in colder temperatures presumably must be in the form of resting eggs.

Of the localities listed in Table I, only Woods Hole, Odessa, and Auckland represent regions where *Penilia* has become well established. There are three reports of its occurrence in northern Japanese waters. The other localities represent simply isolated records which could perhaps be looked on as abnormal oc-



TABLE I

| Locality  | <i>Penilia</i> reported by     | Mean surf. water temps. ( $^{\circ}$ C.) |                               |                 | Authority for temperatures |
|---|--------------------------------|--|-------------------------------|-----------------|----------------------------|
|   |                                | Coldest month                            | Warmest month                 | Annual          |                            |
| Woods Hole, 1945-1951   | Present paper                  | Feb.,<br>0.7 $^{\circ}$                  | Aug.,<br>21.8 $^{\circ}$      | 11.5 $^{\circ}$ | 1                          |
| Woods Hole, 35 years of period 1885-1941                            | No report                      | Feb.,<br>-0.2 $^{\circ}$                 | Aug.,<br>21.1 $^{\circ}$      | 10.4 $^{\circ}$ | 2                          |
| Lat. 40 $^{\circ}$ N., 175 km. south of Woods Hole                  | No report                      | March,<br>6.4 $^{\circ}$                 | Aug.,<br>20.6 $^{\circ}$      | 13.0 $^{\circ}$ | 3                          |
| Dutch coast, 52 $^{\circ}$ 22'N., 4 $^{\circ}$ 20'E.                | Cattley and Harding            | Feb.,<br>3.5 $^{\circ}$                  | Aug.,<br>17.5 $^{\circ}$      | 10.2 $^{\circ}$ | 4                          |
| Near Odessa, Black Sea  | Zagorowsky (see Steuer, 1933b) | Feb.,<br>1.1 $^{\circ}$                  | July-Aug.,<br>22.2 $^{\circ}$ | 13.5 $^{\circ}$ | 3                          |
| Muroran, Hokkaido, Japan  | Tanita, Kato, and Okuda        | March,<br>2.2 $^{\circ}$                 | Aug.,<br>21.7 $^{\circ}$      | 11.0 $^{\circ}$ | 3                          |
| Near Cape Town, S. Africa, 35 $^{\circ}$ 13'S., 20 $^{\circ}$ 17'W. | Rammner                        | July,<br>15.2 $^{\circ}$                 | Jan.,<br>20.6 $^{\circ}$      | 18.2 $^{\circ}$ | 3                          |
| Cook Strait, New Zealand  | Steuer, 1933a                  | July,<br>10.0 $^{\circ}$                 | Feb.,<br>16.1 $^{\circ}$      | 13.2 $^{\circ}$ | 5                          |
| Auckland, New Zealand   | Krämer.<br>Fuller.             | July,<br>12.1 $^{\circ}$                 | Feb.,<br>21.0 $^{\circ}$      | 16.7 $^{\circ}$ | 6                          |

## Authorities for temperatures in Table I

1. Calculated from monthly mean surface temperatures in the years 1945-1951 at the Woods Hole Oceanographic Institution dock, consulted through the kindness of Mr. Dean F. Bumpus. Closely similar figures for the years 1945-1950 have been published by the U. S. Coast and Geodetic Survey (Publ. No. TW-1, 1951).

2. Calculated from monthly and annual mean surface temperature records, very kindly supplied by Mr. John B. Colton, U. S. Fish and Wildlife Service, Woods Hole. Records are not available for the period 1915-1932, nor for a few other scattered years.

3. Figures for each month read from: World Atlas of Sea Surface Temperatures, H.O. No. 225, Hydrographic Office, U. S. Navy, Washington, D. C.: 50 p., 1944.

4. Figures for each month read from: Böhnecke, G., and G. Dietrich, 1951. Monatskarten der Oberflächentemperatur für die Nord- und Ostsee und die angrenzenden Gewässer. Deutsches Hydrographisches Institut, Hamburg: 18 p.

5. Figures for each month read from charts in: Monthly sea surface temperatures of Australian and New Zealand waters; Marine Branch Meteorol. Office, Air Ministry, London; M.O.M. 482: 14 p., 1945.

6. Calculated from monthly mean surface temperatures for each of the years ending April, 1929, to April, 1941, in: Report on Fisheries, New Zealand Marine Dept., years ending March, 1931, to March, 1941.

currences. With this in mind it might appear that only where the mean surface temperature in the warmest month reaches or exceeds  $21^{\circ}$  can *Penilia* become permanently established. Perhaps such warm temperatures are necessary to permit the building up of a minimal population density, sufficient to assure the survival of at least some individuals, or resting eggs, through the winter.

In localities such as Woods Hole and Odessa, where temperatures are adequate in summer but very low in winter, one must consider the possibility of repopulation each spring from warmer waters to the south. This probably would have to be by currents, if we accept the assumption, presented earlier, that resting eggs can be caught up in wind-driven spray only when newly released, which would be chiefly in late summer and autumn. Unfortunately our knowledge of non-tidal surface currents south of the New England coast is very incomplete. The complexity of the situation is well presented by Haight (1942). More recent information is given by Zinn (1950), and an analysis of the complex tidal currents near Woods Hole has been presented by Redfield (1953). Rather detailed charts of non-tidal surface currents in the waters east of the United States were published for each month of the year by the German "Oberkommando der Kriegsmarine" (1943), but must include much that is based only on conjecture. In general, it would seem that coastal organisms to the south of New York would stand little chance of being brought to New England waters; organisms from the Gulf Stream, directly to the south of New England, such as the siphonophore *Physalia*, certainly are brought to the New England coast in some summers, but the existence every year of such currents from the south is highly doubtful.

Table I shows that if *Penilia* occurred just beyond the continental shelf to the south of Woods Hole, it would encounter minimal winter temperatures of about  $6.4^{\circ}$ . But summer temperatures there might not be adequate for a high rate of reproduction; the presence of *Penilia* so far from land would not be expected; and the annual occurrence of suitable currents to bring the organisms to the coast seems rather unlikely.

Thus it appears probable that *Penilia* is now a year-round inhabitant of Woods Hole waters. If so, the resting eggs must be able to withstand winter temperatures down to below zero (the mean surface temperature at Woods Hole for January, 1948, was  $-1.2^{\circ}$ ; a temperature of  $-2.8^{\circ}$  was recorded on one occasion in 1945). In effect this would mean that the only temperature requirement for *Penilia* is a summer temperature of perhaps  $21^{\circ}$  or above, with lower temperatures possible in regions where a high population density is not necessary to assure survival through the winter.

From Table I it will be seen that water temperatures at Woods Hole in the period 1945-1951 averaged slightly higher than in previous years. However, the facts stated above make it unlikely that the slightly colder winters of the past were responsible for the absence of *Penilia* from New England waters.

#### DISCUSSION

It must remain for future investigation to provide more certain data, and in particular to discover an explanation for the apparent absence of *Penilia* from so many regions that would appear favorable for its development. Doubtless its occurrence has frequently been overlooked, but in regions where the plankton has been inten-

sively studied one would expect it to be reported if present. Thus at both Woods Hole and Naples, *Penilia* is now abundant, but would seem to have been absent at least for many years in the past.

Possibly such sudden inroads into new areas have been preceded by a process of genetical pre-adaptation to wider temperature limits, as reported for fresh water Cladocera by Brown (1929). (See also Johnson, 1952.) Perhaps, too, the production of resting eggs by *Penilia* occurs only in a few genetic stocks, of localized distribution. Reproduction by parthenogenesis alone might lead to local extinction, as noted earlier, and the failure to produce resting eggs presumably would prevent colonization of areas where water temperatures are low in winter. Many other interesting possibilities could be suggested. The whole question of how the population cycle of *Penilia* may be related to the population cycles of other planktonic organisms remains virtually an untouched field. Some data relative to this problem will be found in the papers of Dakin and Colefax (1933), Deevey (1952b), Massutí Alzamora (1949), and Sheard (1949).

#### TESTS FOR BIOLUMINESCENCE

A report concerning *Penilia* that would be of considerable interest if it could be confirmed is contained in the paper of Dakin and Colefax (1940), who state that *Penilia* "appears to be one cause of luminescence in our plankton." They add that "no distinct luminous organs have been noticed." In August, 1953, I attempted to repeat Dakin and Colefax's observation, with wholly negative results. Dark-adapted specimens of *Penilia* were picked out from a freshly caught plankton sample, and were observed in the dark in groups of ten or more concentrated in a small volume of water. Stimuli used to provoke luminescence were mechanical stirring with a glass rod, drop by drop addition of formalin, ammonium hydroxide, alcohol, and glycerine, the make and break passage of an electric current at various intensities from an inductorium, and exposure to ammonia vapor, the specimens in this case being supported in air on a piece of bolting silk. These stimuli include the principal ones used by Giesbrecht (1895) in his search for luminescent copepods. In no case did any of the specimens of *Penilia* exhibit bioluminescence. This was in contrast to other unidentified microscopic organisms, which luminesced brightly in samples of the plankton from which all specimens of *Penilia* had been carefully removed.

It seems reasonably certain that *Penilia* is not luminescent at Woods Hole in the month of August. However, Giesbrecht found that copepods at Naples, if they luminesce at all, do so for the most part only in the winter. Dakin and Colefax observed *Penilia* in Australian waters at all times of the year, and perhaps it was in the winter that their specimens seemed to be luminescent. If *Penilia* is self-luminous at times, it is probably unique in this respect within the class Branchiopoda (Harvey, 1952), and it might be cited as an especially interesting example of the general rule that among aquatic organisms the only ones that are luminescent are marine.

#### SUMMARY

1. *Penilia* has recently become a regular member of the summer plankton off the southern coast of New England, much farther north than would formerly have been expected.

2. Its reproduction in New England waters is mainly by ovoviviparous parthenogenesis, but males also occur, together with females bearing fertilized, resting eggs. There is reason to believe that the species overwinters locally in the form of resting eggs, rather than being brought in each year by wind or currents.

3. The poleward distribution of *Penilia* seems to be limited only by the need of a certain minimum water temperature in summer. Adults can survive at temperatures down to below 9° C., and are able to reproduce at and perhaps below 16° C. But the species has not become permanently established except in areas where summer water temperatures exceed 21° C. The resting eggs probably can survive winter temperatures of below -2° C.

4. *Penilia* is found in every ocean of the world, often as one of the dominant plankton organisms, yet it is absent from many regions where it might be expected to thrive. Possible reasons for this discontinuous distribution are discussed. Sudden appearances of *Penilia* in new areas perhaps are the result of recently laid, resting eggs becoming caught up in wind-driven spray.

5. The restriction of *Penilia* to coastal waters may be because the resting eggs sink to the bottom. Salinity is not the limiting factor, since *Penilia* has been found in salinities ranging from fresh water to 49‰.

6. *Penilia* shows no obvious responses to light or to pressure which might account for its restriction to surface waters.

7. The fact that *Penilia* is the only filter-feeding branchiopodan to have become truly marine, may possibly be because in sea water it is difficult for members of this group to maintain the necessary turgor within their phyllopodia.

8. A report that *Penilia* is bioluminescent could not be confirmed for specimens examined in August at Woods Hole, Massachusetts. The possibility remains that in some localities it may be luminescent in winter.

#### LITERATURE CITED

An asterisk denotes papers referring to *Penilia*. All papers are listed that could be found recording the presence of *Penilia*, if not already listed by Calman, 1917-23, Steuer, 1933b, or Lochhead, 1936-7. I am much indebted to Dr. Mary Sears for certain references, and to Miss Velma Cochran for aid in searching the literature.

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